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Macro benthic community assemblage before and after the 2007 tsunami and earthquake at Paracas Bay, Peru

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ABSTRACT

Macrobenthic soft bottom community assemblages were studied from December 2006 to December 2007 at Paracas Bay (Atenas Beach, 13°45' S, 76°17' W, Peru), including the period of the tsunami of 15 August 2007, providing a unique opportunity to assess the effects of this type of natural disturbance in soft bottom marine ecosystems. The results show that the tsunami affected the soft bottom community assemblage by changing the sediment granulometry, the biomass and abundance of epifaunal species, and by increasing the silt proportion. The event affected all functional groups, resulting in an increased numbers and biomass of filter feeder and grazers that were followed soon after by predators during the post-tsunami period. A similar pattern was observed for biomass and the abundance of infaunal species without changing the functional groups. The slow recovery observed after four months was likely related to the loss of sediment stability. In summary, there were differences in the structure and composition of soft bottom macrofaunal assemblages before and after the earthquake and posterior tsunami disturbance, forcing benthic communities to initiate re-colonisation processes.

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1. Introduction

The term disturbance is broadly defined as an uncommon, irregular or discrete event that causes abrupt structural changes that affect resources or the physical environment (see Pickett and White, 1985) in natural communities, moving them away from static or near-equilibrium conditions (e.g., Sousa, 1984). Disturbances not only affect resident organisms, but also directly or indirectly alter the biological or physical environment of individuals that re-colonise the affected area following the event. These environmental alterations can strongly influence subsequent patterns of re-colonisation and succession (Connell et al., 1997). Direct changes to the physical environment include alterations to the substrate and local topography, which in turn affect currents, light levels, and sedimentation rates (Minoura and Nakaya, 1991; Noda et al., 2007). Direct impacts to the biological environment include changes in the abundance and distribution of non-resident species that potentially interact with the residents. The biological environment is indirectly modified by disturbances that alter the local abundance of refuges, food, or nutrients available to resident species or others that interact with them (Sousa, 2001).

A tsunami is a rare disturbance within marine communities (Sousa, 2001), but it possesses a high intensity and/or energy (Krishankutty, 2006; Bourrouilh-Le Jan et al., 2007). One of the most significant phenomena related to tsunami is the large-scale removal of coastal sediment, followed by widespread deposition of marine sand on coastal lowlands (Minoura and Nakaya, 1991; Bourrouilh-Le Jan et al., 2007). In addition, tsunami waves can re-suspend, transport, and redeposit sediments on the sea floor as a result of repeated incoming and outgoing flows (Noda et al., 2007). These processes have great potential to affect coastal benthic communities.

Several studies have described the effect of tsunamis on marine communities, especially after the 26 December 2004 tsunami that struck the Asian coastline. Results from these studies showed direct effects of wave forces and indirect effects of sedimentation on a seaweed community with a slow post-tsunami recovery in India (Mantri, 2005, 2006) and Thailand (Prathep et al., 2007). Destruction caused by direct and indirect effects of sedimentation was also observed on coral reefs in Thailand (Chavanich et al., 2005) and India, including the post-event infestation of coral reefs by disease-producing fungi (Kumaraguru et al., 2005). Similar destruction occurred within seagrass beds and associated macrofaunal communities in the Andaman Sea, Thailand (Whanpetch et al., 2010), forcing benthic communities to start re-colonisation processes. Mangroves were important natural barriers at several sites where fewer negative effects on their associated communities were observed (i.e., Sri Lanka: Dahdouh-Guebas et al., 2005; Cuddalore District in Tamil Nadu, India: Danielsen et al., 2005). Tsunami-disturbed

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marine communities offer excellent opportunities to test available theories on disturbance (Krishankutty, 2006).

On 15 August 2007, an earthquake with a moment magnitude (M_w) of 8.0 occurred off the coast of central Peru (13.76° S, 76.97° W) at a depth of 39 km. The earthquake lasted 3.5 min and was located at the interface between the South American Plate and the subducting Nazca Plate (Rodríguez-Marek et al., 2007). The earthquake generated a tsunami with locally-focused runup wave heights of up to 10 m (Fritz et al., 2008). Three tsunamis with the largest runup heights were reported south of the Paracas Peninsula (see Fig. 1) in a sparsely populated desert area. Numerical modelling of the earthquake and tsunami suggests that a region of high slip near the coastline was primarily responsible for the extreme runup heights (Fritz et al., 2008). Atenas Beach (Fig. 1), an area located inside Paracas Bay, was shielded by the Paracas Peninsula, meaning that tsunami waves did not propagate with high intensity northward from the high slip region. In this area, runup height was 2 to 3 m (Fritz et al., 2008). As a result, flooding occurred along a stretch of coastline from Paracas north to Miraflores in the city of Lima.

After observing this event we hypothesised that a tsunami had the potential to negatively affect a benthic community and result in changes to community characteristics and the macrofaunal re-colonisation process (i.e., species biomass, abundance, diversity, dominance, richness, composition). Thus, the main objective of this study was to evaluate the immediate effect of tsunami disturbance on soft bottom macrofaunal assemblages located at Atenas Beach in Peru.

2. Materials and methods

2.1. Study area and sampling

The study was conducted on the subtidal soft bottom at Atenas Beach inside Paracas Bay ($13^\circ 45$ S, $76^\circ 17'$ W; Fig. 1), Peru. The bay

encompasses 30 km of coastal littoral areas, and it has a maximum depth of 12 m. The nutrient concentration is the highest along the Peruvian coast, supported by the “San Juan” upwelling and water mass circulation inside the bay (Zuta and Guillén, 1970). The area showed enrichment by organic matter (Mendo et al., 2000; De la Cadena Mory, 2005), mainly due to the input of fishery effluents (fish meal and fish oil factories) which resulted in harmful algal blooms, which have a synergistic effect on the quality of the water column and the sediments over time (Mendo et al., 2000; Cabello et al., 2002). These conditions often cause mortality within benthic species (i.e., scallops, Mendo et al., 2000). The regional climate is typical of the Peruvian arid coastal desert, with an average temperature of 19.5° C, and 12 mm of rain per year (Galán de Mera et al., 2004).

Bimonthly sampling was performed by scuba diving at a depth of 5 to 8 m from December 2006 to December 2007, which included the earthquake and tsunami of 15 August 2007. This sampling method resulted in an unbalanced sample with four samples taken before the event and two taken after the event. Given that the tsunami-impacted area was very large, it was impossible to set up control areas for a comparative study (i.e., BACI design, Underwood, 1994).

2.2. Sediment characteristics

To evaluate possible differences in sediment characteristics before and after the tsunami event, five sediment samples (cores of 5 cm diameter and 35 cm deep) were collected each month. Organic matter content (OM) was defined as the difference between dry weight (80° C to constant weight) and the ash-free dry weight (450° C for 8 h) of each sediment sample. A grain size frequency distribution was obtained by sieving a subsample through a series of seven meshes (>2 mm, 2–1 mm, 1–0.5 mm, 0.5–0.25 mm, 0.25–0.125 mm, 0.125–0.063 mm, 0.063–0.0039 mm, <0.0039 mm). To evaluate the

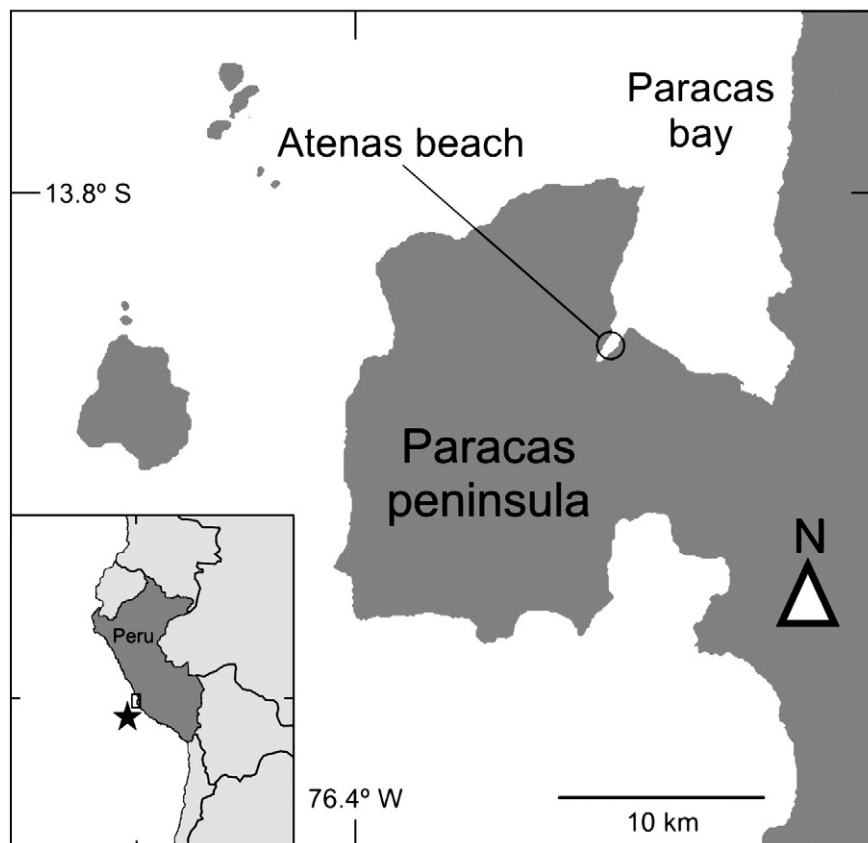


Fig. 1. Map indicating the study area, Atenas Beach, inside Paracas Bay at Central Peru. Star: indicating the earthquake epicentre with a moment magnitude (M_w) of 8.0 centred off the coast at 13.76° S, 76.97° W at a depth of 39 km, lasted 3.5 min.

null hypothesis that there was no difference between sediment organic matter content and size fractions throughout the year, a one-way analysis of variance (ANOVA) with subsequent Tukey's HSD tests was used. The proportion datasets (e.g., grain size) were arcsine-transformed (Zar, 1999). Prior to using the ANOVA, data were tested for normality and homogeneity of variances (Zar, 1999). To meet ANOVA assumptions, data were transformed until the best fit was found, in this case to $1/X^3$.

2.3. Community characteristics

To evaluate the specific composition and relative abundance of the subtidal benthic organisms at Atenas Beach, ten sample cores (10 cm diameter and 25 cm depth) were taken from the soft bottom on each sampling date. Each sample was divided between the bottom surface (up 1 cm) epifaunal species and the macroinfauna inhabiting the sediment below the surface. Each sample was sieved throughout 500 μm mesh and the community composition was analysed.

All organisms in each species were counted, the total mass (TM) determined, and the soft mass was dried at 80 °C to a constant weight with a precision of ± 0.01 g.

Each assemblage was evaluated for the same attributes of community characteristics, including total number of individuals (N), total number of species (S), the total biomass (B), diversity indices such as the Shannon–Wiener diversity index (using Ln ; (H')), Margalef's index (d), Pielou's evenness index (J'), and the Simpson index (λ). Additionally, the Abundance/Biomass Comparison (ABC) method (Clarke and Warwick, 2001) was performed to determine levels of disturbance of the benthic macrofauna community before and after the tsunami event.

To compare species assemblages during the year, four separate sets of multivariate and univariate analyses were performed. Epifauna and infauna were analysed with abundance and biomass data. Bray–Curtis similarity matrices using fourth root-transformed data were calculated and non-metric Multidimensional Scaling (nMDS) ordinations were used to provide visual representations of sample similarities (Clarke and Warwick, 2001). One-way analyses of similarities (ANOSIM) were performed (Clarke, 1993) to test for differences among sampling month with R as the coefficient of similarity. The percent contribution of each taxon to patterns of dissimilarity between months was calculated (Clarke, 1993). Taxa contributing at least 10% of dissimilarity were considered significant (Bulleri, 2005). The abundance of these taxa was then analysed by Kruskal–Wallis non-parametric analyses.

Additionally, epifaunal and infaunal organisms were also classified according to their feeding habits (grazers, suspension-feeders, deposit-feeders, and predators/scavengers) and mobility (sessile and mobile). Organisms were classified based on the morphological characteristics of specimens and the available literature (see Valdivia and Thiel, 2006). Separate Kruskal–Wallis tests, followed by non-parametric Tukey-type tests, were performed to analyse temporal differences in feeding guilds, mobility groups and total abundance of organisms.

3. Results

3.1. Sediment characteristics

The percentage of organic matter was higher in Jun-07 (one-way ANOVA, $F_{5,24} = 8.07$, $p < 0.001$) than all other months. Mean grain size varied throughout the year ($F_{5,12} = 47.37$, $p < 0.05$). The smallest mean grain size was observed in Jun-07 and Oct-07, and both were different from the other months (Tukey HSD test, $p < 0.05$), whereas the largest mean grain size occurred in Dec-06, Feb-07 and Apr-07. However, only Apr-07 resulted in a higher grain size than Dec-07 (Tukey HSD test, $p < 0.05$). The smallest mean grain size observed in Jun-07 was caused by an increase of the clay fraction (< 0.0039 mm), which coincided with the higher OM. The sea floor area was covered by very fine sand, which changed after the tsunami event (Oct-07), resulting in an increase of the silt fraction (Table 1).

3.2. Community characteristics

The epifaunal assemblage was represented by 22 species (Table 2). The Shannon–Wiener diversity index (H') varied from 0 (Apr-07 and Jun-07) to 0.73 (Oct-07) during the post-tsunami period, showing no difference among months (Anova, $F = 1.68$, $p > 0.05$). The Margalef's index (d) showed no difference between months with a minimum value of 0.31 in Feb-07 and a maximum of 0.99 for Dec-06 and Oct-07. Pielou's evenness index (J') showed a difference (Anova, $F = 8.63$, $p < 0.001$) between the post-tsunami month of Oct-07 (minimum value 0.45) and the other months (values between 0.89 Dec-06, Dec-07 and 0.97 Feb-07; Tukey HSD test, $p < 0.05$). The Simpson index (λ) showed no difference among months (Anova, $F = 1.28$, $p > 0.05$) with minimum value of 0.30 in Feb-07 and the maximum of 0.61 at Dec-06. The Abundance/Biomass Comparison (ABC) method showed that the abundance curve lies below the biomass curve throughout all analysed months (Fig. 2a).

The structure of the epifaunal assemblage varied throughout the year taking into consideration both the abundance and biomass data ($R = 0.44$ and 0.45 , respectively, $p < 0.05$; see Fig. 3a, b). Oct-07 was different from all other months. Moreover, when considering abundance data, Dec-07 was different from Dec-06 (all $p < 0.05$, ANOSIM pairwise tests).

Many of the dissimilarities among sampling dates could be accounted for by three taxa. The barnacle *Balanus laevis*, the crab *Eurypanopeus transversus*, and the polychaete *Lumbrineris* sp. distinguished consistently among months. *B. laevis* was only found after the tsunami, reaching its maximum abundance and biomass in Oct-07 ($H_{5,60} = 44.8$ for both, $p < 0.05$, Fig. 4a, b). *Lumbrineris* sp. abundance and biomass was highly variable during the year, reaching its highest values in Dec-07. However, the values were not different from those observed in Dec-06 and Jun-07 ($H_{5,60} = 18.17$ for abundance and 16.9 for biomass, $p < 0.05$, Fig. 4). Furthermore, when considering biomass data, *Argopecten purpuratus*, was also found to be an important cause of differentiation, appearing only immediately after the tsunami ($H_{5,60} = 32.6$; $p < 0.05$, Fig. 4). Contrarily, when analysed with

Table 1

Granulometry of Atenas beach during the year. Values for sediment fractions are expressed in percentage. Dashed line represents tsunami event.

Month	Mean grain size (mm)	Median grain size (mm)	Very coarse sand (2–1mm)	Coarse sand (1–0.5mm)	Medium sand (0.5–0.25mm)	Fine sand (0.25–0.125mm)	Very fine sand (0.125–0.062mm)	Silt (0.062–0.0039mm)	Clay (<0.0039mm)
Dec-06	0.236	0.238	4.12	8.13	12.08	18.39	27.13	24.07	6.08
Feb-07	0.243	0.242	4.4	7.34	12.36	21.51	30.89	18.36	5.12
Apr-07	0.251	0.246	5.2	7.82	11.98	19.28	27.62	22.22	4.78
Jun-07	0.214	0.216	2.78	7.18	12.66	16.93	36.73	15.66	8.07
Oct-07	0.204	0.203	2.63	7	11.64	18.68	25.02	28.87	6.16
Dec-07	0.229	0.229	3.8	7.44	11.77	20.68	27.17	23.31	5.83

Table 2
Classification according to feeding habits (grazers, suspension-feeders, deposit-feeders, and predators/scavengers) and mobility (sessile and mobile) of all species found.

	Taxa	Epifauna	Infauna	Feeding	Mobility	Reference
Polychaete	<i>Lumbrineris</i> sp.	X	X	Predator	Mobile	Tokeshi and Romero, 2000
	Dorvilleidae	X		Deposit feeder	Mobile	Fauchald and Jumars, 1979
	Capitellidae	X	X	Deposit feeder	Mobile	Valdivia and Thiel, 2006
	Eunicidae	X		Predator	Mobile	Fauchald and Jumars, 1979
	Nereidae	X		Predator	Mobile	Fauchald and Jumars, 1979
	Hesionidae	X		Grazer	Mobile	Fauchald and Jumars, 1979
	Chaetopteridae	X		Suspension feeder	Sessile	Fauchald and Jumars, 1979
Ophiuroidea	<i>Ophiactis</i> sp.	X		Deposit feeder	Mobile	Taylor et al., 2008
Actinia	Actinia	X		Suspension feeder	Sessile	Taylor et al., 2008
Gastropod	<i>Nassarius gayi</i>	X	X	Predator	Mobile	Taylor et al., 2008
	<i>Nassarius dentifer</i>	X		Predator	Mobile	Taylor et al., 2008
	<i>Crepidula = Crepipatella dilatata</i>	X		Suspension feeder	Sessile	Valdivia and Thiel, 2006
Bivalve	<i>Argopecten purpuratus</i>	X		Suspension feeder	Sessile	Pacheco and Garate, 2005
Barnacle	<i>Balanus laevis</i>	X		Suspension feeder	Sessile	Pacheco and Garate, 2005
Decapod	<i>Synalpheus spinifrons</i>	X		No information	Mobile	
Crab	<i>Eurypanopeus transversus</i>	X	X	Deposit feeder	Mobile	Taylor et al., 2008
	<i>Alpheus</i> sp.	X		Deposit feeder	Mobile	
	Amphipoda	X		Deposit feeder	Mobile	Rupert and Barnes, 1995
	Caprellidae	X		Grazer	Mobile	Perrett et al., 2006
Amphipod	Gammaridae	X	X	Grazer	Mobile	Parker et al., 1993
	Ischyroceridae	X		Suspension feeder	Sessile	Thiel and Vásquez, 2000
	Ingolfiellidea	X		No information	Mobile	

univariate non-parametric tests, *E. transversus* showed no temporal variation in abundance or biomass ($H_{5, 60} = 7.8$ and 6.5 , respectively; $p > 0.05$, Fig. 4).

The infaunal assemblage was represented by five species (Table 2). The Abundance/Biomass Comparison (ABC) method showed that the abundance curve lies below the biomass curve throughout its length in Dec-06 (Fig. 2b); given the presence of a unique species, no statistical analyses could be performed during the remainder of the sampling months.

The infauna assemblage was also different throughout the year ($R = 0.6$ for abundance data and 0.62 for biomass data, $p < 0.05$; see Fig. 3c, d). Oct-07 and Dec-07 were different from the other months, Jun-07 was different from Dec-06, and, when considering biomass data, Feb-07 was different from Dec-06 (all $p < 0.05$, ANOSIM pairwise tests).

All five species found in the infauna resulted in cause of differentiation. The polychaete *Lumbrineris* sp. disappeared completely after the tsunami ($H_{5, 60} = 15.8$; $p < 0.05$; Fig. 5a, b). The polychaete Capitellidae was rare, as it was found in only one sample in Dec-06. Gammarid amphipods were also found in Dec-06. *E. transversus* appeared in two samples, in Dec-06 and Jun-07. Finally, the gastropod *Nassarius gayi* was only found after the tsunami ($H_{5, 60} = 29.2$; $p < 0.05$; Fig. 5).

After analysing the functional groups, it was found that, in general, almost all epifaunal groups were more abundant in Oct-07 than all other months, and they showed the lowest abundance levels in Feb-07, Apr-07 and Jun-07 (Fig. 6). An exception was predatory species, for which the abundance in Dec-07 was greater than in Feb-07 and Apr-07 ($H_{5, 60} = 21.7$; $p < 0.05$). In Oct-07, the abundance of deposit-feeders was greater than in Jun-07 ($H_{5, 60} = 15.1$; $p < 0.05$). Suspension-feeders reached their greatest abundance in Oct-07 ($H_{5, 60} = 42.97$; $p < 0.05$), and they represented the trophic group with the highest abundance overall. Despite a drop in Dec-07, both months (Oct-07 and Dec-07) were similar. The grazer abundance observed in Oct-07 was also greater than in Feb-07, Apr-07 and Jun-07 ($H_{5, 60} = 27.1$; $p < 0.05$).

In Oct-07, mobile organisms were also more abundant than in Feb-07, Apr-07 and Jun-07 ($H_{5, 60} = 27.46$; $p < 0.05$), and sessile species, constituted almost exclusively by suspension-feeders, showed the same pattern ($H_{5, 60} = 43.14$; $p < 0.05$). The greatest total abundance was observed in Oct-07, but this measurement was no different than in samples taken in Dec-06 and Dec-07 ($H_{5, 60} = 38.75$; $p < 0.05$).

There were more infaunal grazers in Dec-06 ($H_{5, 60} = 15.51$; $p < 0.05$), but this was likely due to the presence of Gammarid amphipods. No additional differences were found with respect to feeding guild ($H_{5, 60} = 6.83$ and 7.31 for predators and deposit-feeders, respectively; $p > 0.05$ for both) or total abundance ($H_{5, 60} = 3.1$; $p > 0.05$). No suspension-feeders were found, and all infaunal organisms were mobile.

4. Discussion

Our results show that the soft bottom community assemblage of the study site has been affected by the disturbance produced by an earthquake and subsequent tsunami. The tsunami event produced changes in sediment granulometry, enhancing silt sediments indicating their recent transportation. The epifaunal assemblage showed higher levels of biomass and abundance after the event. The functional groups also changed, demonstrating an initial succession process among trophic groups during the post-tsunami period. A similar pattern was observed for infaunal assemblages in relation to biomass and species abundance. These changes did not affect the functional groups, but they continued to influence the bottom community four months after the event.

The sea bottom of the inner shelf at a water depth of less than 30 m is always affected by physical processes such as tidal currents and storm waves (e.g., Komar, 1976). Thus, influences other than the tsunami (Noda et al., 2007) are at work upon sea floor sediments, producing vertical changes in grain size frequency distributions and sedimentary structures such as cross-laminae. The sea floor of Atenas Beach was covered by very fine sand, which changed following the tsunami (Oct-07) to a higher proportion of silt. Coarse-grained Tsunami related deposits have been reported within shallow marine environments (van den Bergh et al., 2003) and shallow marine strata (Fujiwara et al., 2000). Similar deposits were observed after the 2003 Tokachi-oki earthquake in southeastern Hokkaido (Japan), an event that generated maximum wave runup heights of 4 m, showing decreases in fine fractions. This was especially important in relation to very fine sand because the event led to the selective erosion of finer particles, which in turn led to an increase in mean grain size on the inner shelf of the northern part of the study area (Noda et al., 2007). However, no coarse-grained 'tsunami deposits' existed in our study area. Atenas Beach inside Paracas Bay was sheltered from the earthquake epicentre by the Paracas Peninsula (Fig. 1), which blocked

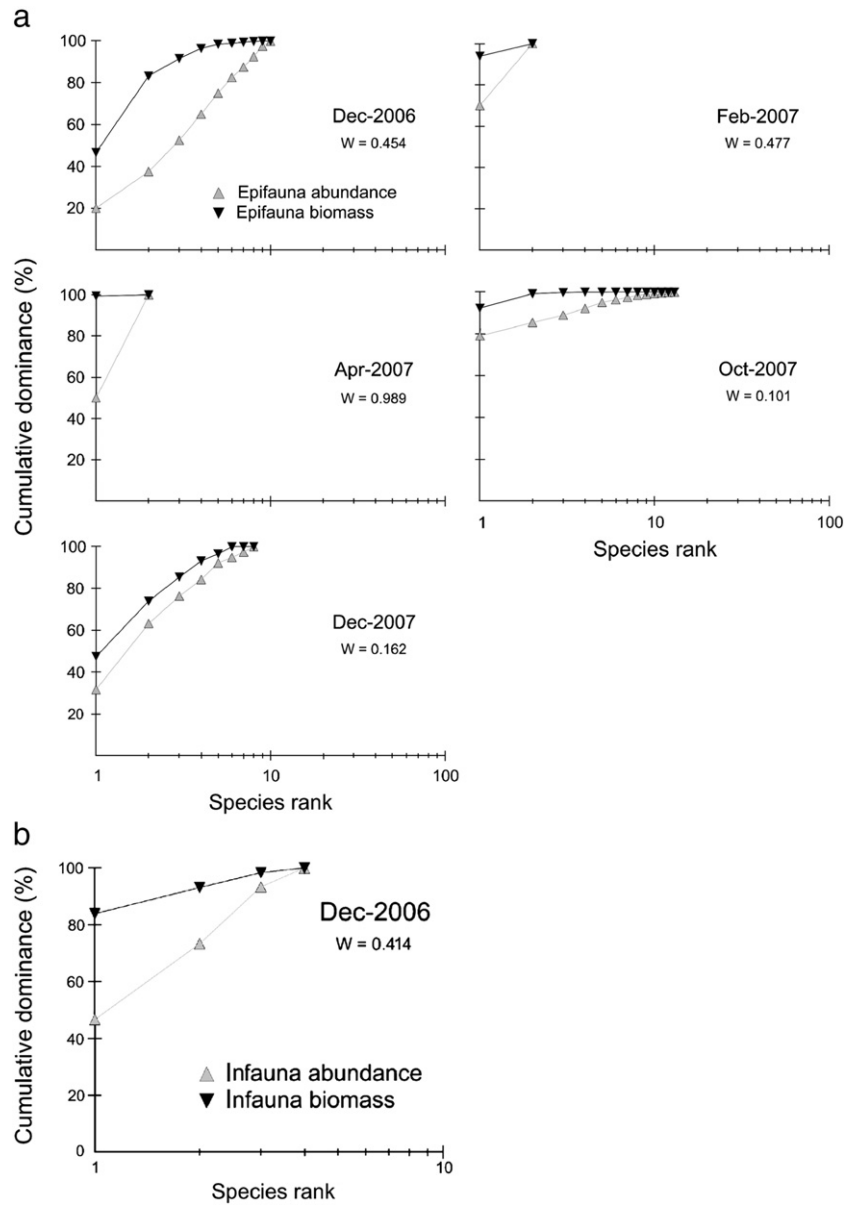


Fig. 2. The Abundance/Biomass Curves (ABC) from (a) epifaunal and (b) infaunal assemblages throughout the year.

tsunami waves from propagating northward from the high slip region, producing height between 2 and 3 m in this area runup (Fritz et al., 2008). Thus, the change in sediment grain size could be interpreted as a decrease of the tsunami wave energy, which transported and deposited finer sediments. A similar situation was observed after the 2003 Tokachi-oki tsunami, which left shelf sediments largely unchanged or slightly finer (Noda et al., 2007). Although changes in sedimentation could be produced by strong currents and storms, for the same study period Atenas Beach exhibited currents with flow rates of 2.81 cm s^{-1} to 11.5 cm s^{-1} near the bottom of the bay (J. Mendo, personal communication; Romero and Orrego, 1983), a rate that is unlikely to cause other sedimentation change (Hill et al., 2004).

The input of organic matter to the bay is produced by year-round fishery activity (Mendo et al., 2000; Cabello et al., 2002; De la Cadena Mory, 2005). We observed that this input (highest values in Jun-07) did not change after the tsunami event. The lowest mean grain size observed in Jun-07 was produced by an increase of the clay fraction, which coincided with higher amounts of OM.

When a community is disturbed, conservative species generally fare worse than opportunists (Huston, 1979; Rosenberg et al., 1983;

Dittmann et al., 1999). Thus, when a community is stressed because of a disturbance, the distribution of number of individuals among species behaves differently from the distribution of the biomass among species (Clarke and Warwick, 2001). The initial conditions of the Paracas system indicate that in the soft bottom benthic community biomass is dominated by one or a few large species. Although these few species raise the biomass curve, each is represented by only a few individuals, meaning that they do not dominate the abundance curve (Clarke and Warwick, 2001). This trend is shown in Fig. 2, where the abundance curve lies below the biomass curve throughout its length (epifauna and infauna). During the post-tsunami time period, these Abundance/Biomass Curves indicated that epifauna experienced fewer differences between curves, but they exhibited a similar pattern, indicating that the physical disturbance produced by the tsunami had indeed altered this community. Both organic enrichment and physical disturbance of the sediment are important elements influencing the structure of benthic communities (Huston, 1979; Widdicombe and Austen, 2001).

Analysis of the epifaunal community showed that dominance by individual species and trophic groups before and after the tsunami

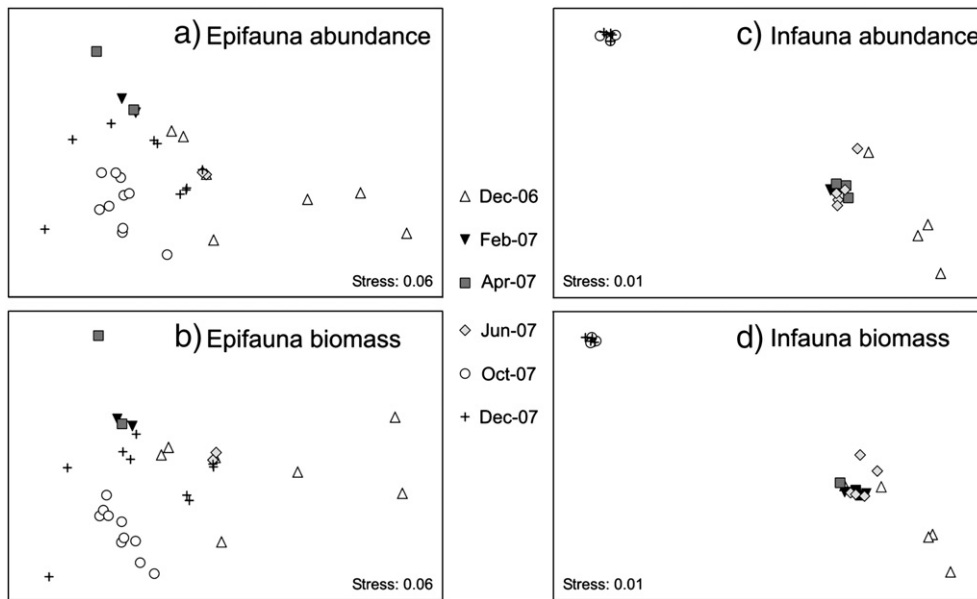


Fig. 3. Non-metric Multidimensional Scaling (nMDS) plots of data comparing (a) epifaunal abundance, (b) epifaunal biomass and (c) infaunal abundance, (d) infaunal biomass assemblages throughout the year.

differed considerably. The dominant epifaunal species before the tsunami were the polychaete *Lumbrineris* sp. and the crab *E. transverses*, followed by Gamarid amphipods and polychaetes Nereidae and Capitellidae. Each species overwhelmingly dominated both number and biomass, which would be predicted for an area with hypoxic condition and high organic matter (Lancellotti and Stotz,

2004). Immediately after the tsunami, these species became less dominant and the polychaete *Lumbrineris* sp., the scallop *A. purpuratus* and the barnacle *B. laevis* became more common. The last species living on hard substratum was possibly scraped off by the great turbulence, carried to Atenas Beach, and deposited in the subtidal soft sediment. However, these differences were observed two months after the event

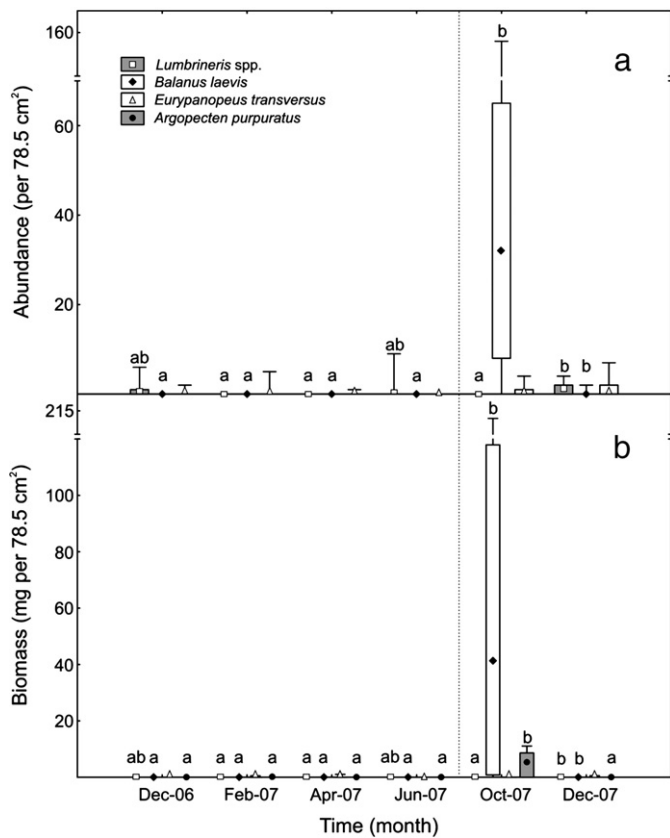


Fig. 4. Median a) abundance and b) biomass of most important differentiators from the epifauna at Paracas Bay. Here and thereafter, the boxes are constructed with 25th to 75th percentiles; whiskers, 5th to 95th percentiles. Dashed line represents the tsunami event. Different letters denote significant differences.

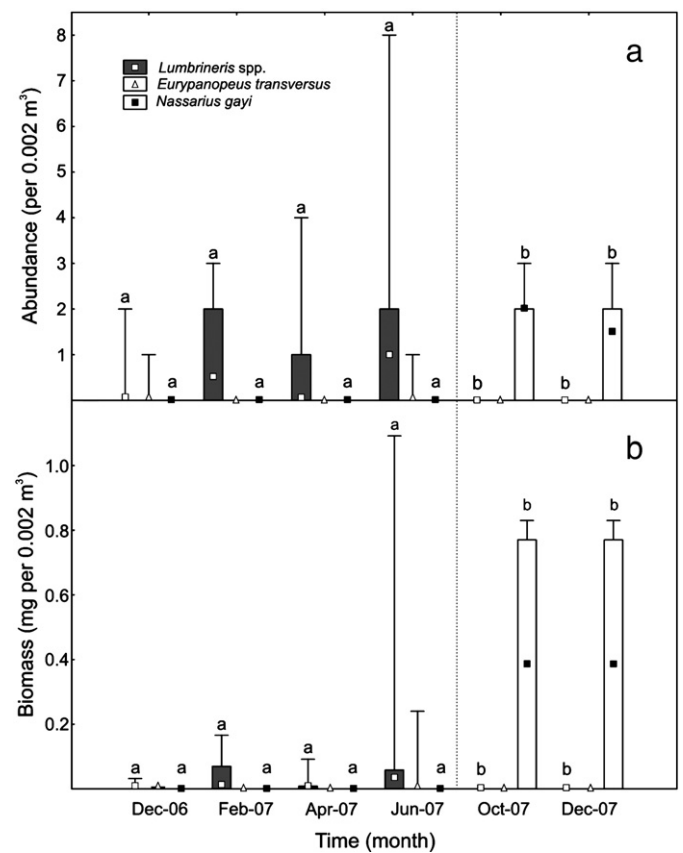


Fig. 5. Median a) abundance and b) biomass of the most important differentiators from the infauna at Paracas Bay. Dashed line represents the tsunami event. Different letters denote significant differences.

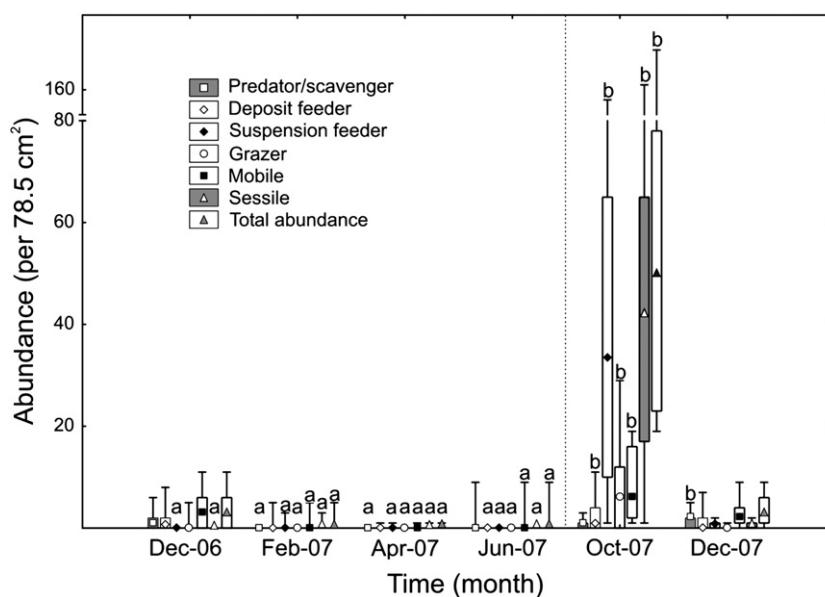


Fig. 6. Median of abundance of the functional groups from the epifauna across the year at Paracas Bay. The dashed line represents tsunami event. Letters denote significant differences.

in the case of biomass (Oct-07) and four months after the event in the case of abundance (Oct-07 and Dec-07).

After analysing the functional groups, in general, we found that almost all epifaunal groups (deposit-feeders, suspension-feeders and grazers) were more abundant immediately after the tsunami (Oct-07). Predators were an exception, showing increased abundance at a later time (Dec-07) and demonstrating an initial succession process between trophic groups (see Roth and Wilson, 1998).

Results pertaining to mobility groups indicated that mobile and sessile organisms (constituted almost exclusively by suspension-feeders) also showed the greatest abundance in Oct-07. Strong water currents can stress organisms and also carry sediments or other objects that may abrade, crush, or break them (Sousa, 2001). Thus, the disturbance caused by the tsunami affected both sediment quality (see above) and benthic assemblage stability by removing the surface sediment layer, forcing benthic communities to begin to re-colonise. A similar pattern was observed with macrofaunal species associated with seagrasses in the Andaman Sea, Thailand (Whanpetch et al., 2010) after the 26 December 2004 tsunami that affected the Asian coastline.

Only five infaunal organisms, all mobile, showed differences in both biomass and abundance between the pre- and post-tsunami sampling dates. The period before the tsunami was characterised by the dominance of the polychaete *Lumbrineris* sp. Rare species, such as the crab *E. transverses*, Gammarid amphipods and the polychaete Capitellidae all disappeared after the tsunami event. However, no difference was observed in the infauna with respect to feeding guild or total abundance, and no suspension feeders were found. The possible effects of physical disturbance on infauna appear to be extremely strong resulting in the unique presence of the gastropod *N. gayi* at post-tsunami period. This opportunistic species favouring hard substrates has been linked to El Niño (EN) and post-EN events (Tarazona et al., 1988, 1996). After strong storms, erosion, deposition, and the bedform movement of sediments are major causes of mortality for infauna (Posey et al., 1996). The most likely mechanisms driving what was observed within this system are changes in sediment characteristics and the deposition of finer sediment during the post-tsunami period, which is reinforced by the appearance of species found on hard substrate that were dragged to the site, such as *N. gayi*. Similar indirect effects of sedimentation were observed within a seaweed community (Mantri, 2005, 2006; Prathep et al., 2007) and

on coral reefs (Chavanich et al., 2005) after the 26 December 2004 tsunami affecting the Asian coast. In all cases, infaunal re-colonisation is predicted to be slow and is related to sediment stability (Posey et al., 1996).

Because the first post-tsunami samples (Oct-07) were not completed immediately following the tsunami, we cannot rule out the possibility that other disturbances influenced community composition during the sampling gap. However, we have no records of strong storms or currents in the study area during this two-month period (J. Mendo, personal observation), which suggests that additional disturbances were unlikely.

In summary, our results show that the tsunami event did not produce differences in the diversity index, but we found clear differences in the structure and composition of the soft bottom macrofauna assemblages before and after the disturbance.

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